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Growth and Stomatal Behavior of Hydroponically Cultured Potato (*Solanum tuberosum* L.) at Elevated and Super-Elevated CO_2

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Summary

Potato cultivars Denali and Norland were grown in a controlled environment under low irradiance and CO_2 partial pressures of 50, 100, 500, and 1000 Pa. The highest CO_2 partial pressures, 500 and 1000 Pa, reduced tuber yield when compared to 100 Pa CO_2. Upper canopy stomatal conductance was greatest at the higher CO_2 partial pressures (500 and 1000 Pa) for both cultivars, and conductance of Denali was consistently higher than Norland. Stomatal conductance tended to decline sooner with plant age at 50 and 100 Pa CO_2 than at 500 and 1000 Pa. Water uptake was also greatest at the higher CO_2 partial pressures, which resulted in lowest water-use efficiencies at 500 and 1000 Pa. These observations suggest that stomatal function under very high CO_2 partial pressures (500–1000 Pa) does not follow known patterns observed at moderate partial pressures (50–100 Pa). Although there is little concern about CO_2 partial pressures reaching extreme levels in the natural environment, this information should be useful for controlled environments or space life support systems (e.g. space vehicles or habitats), where CO_2 partial pressures of 500–1000 Pa are common.

Key words: CELSS, carbon dioxide, Solanum tuberosum, stomatal conductance, water use efficiency.

Abbreviations: CELSS = Controlled Ecological Life Support System; DAP = days after planting; DM = dry mass; HI = harvest index; PPF = photosynthetic photon flux.

Introduction

The National Aeronautics and Space Administration (NASA) is supporting research on bioregenerative life support systems for sustaining humans in extraterrestrial habitats. In such systems, often referred to as Controlled Ecological Life Support Systems (CELSS), higher-plant photosynthesis and transpiration would be used to provide much of the food, O_2, and potable water needed by the habitants.

Tightly closed, human-inhabited spacecraft tend to have CO_2 partial pressures much higher than those of Earth (36 Pa), with levels as great as 1000 Pa having been measured in the US Space Shuttle and Russian Mir space station (D. Wiegrefe, The Bionetics Corp., 1993, personal communication; V. Polyakov, Cosmonaut, 1991, personal communication). Thus plants grown in tightly closed life support habitats may be exposed to very high CO_2 levels.

Because of its nutritional value and high proportion of edible biomass (Tibbitts and Cao, 1992), potato is being tested for use in a CELSS. Controlled environment tests have shown that edible biomass production rates of potato tubers can be significantly greater than the edible component of some seed crops considered for CELSS, e.g. wheat and soybean, when grown at PPF levels ranging from 24–45 mol $m^{-2} d^{-1}$ (Wheeler et al., 1996).

There has been extensive research related to carbon partitioning and tuber growth in potato (Engels and Marschner, 1986 a, 1986 b, 1986 c; Ewing and Struik, 1992; Hannapel, 1991). Yields are known to be affected by several environmental factors, including photoperiod (Steward et al., 1981;

Cao and Tibbitts, 1991; Wheeler and Tibbitts, 1986 a), temperature (Steward et al., 1981; Bennett et al., 1991, Wheeler et al., 1986 b), mineral nutrition (Cao and Tibbitts, 1992; Walworth and Muniz, 1993), and CO_2 concentration (Wheeler and Tibbitts, 1989; Wheeler et al., 1991). In addition, there can be interactions between environmental factors with regard to potato growth. For example, potato yields increased 39 % with CO_2 enrichment (100 Pa or 1000 µmol mol^{-1}) at moderate irradiance (17.3 mol m^{-2} d^{-1}), but these gains in response to CO_2 enrichment decreased as irradiance was increased to 34.6 mol m^{-2} d^{-1} (Wheeler et al., 1991).

Unfortunately, few studies of plant response to CO_2 have included treatments as high as 500 or 1000 Pa. Tomato production was depressed when plants were grown under 500 Pa, as compared to 100 Pa (Hicklenton and Jolliffe, 1980). Wheat and rice seed dry mass dropped about 25 % when grown under 213 vs. 85 Pa CO_2 (2500 vs. 1000 µmol mol^{-1}) (Bugbee et al., 1994). Seed dry mass of soybean cv. McCall was depressed at 200 and 500 Pa, in comparison to 100 Pa, but seed yield of cv. Pixie was unaffected at CO_2 partial pressures between 50 and 500 Pa (Wheeler et al., 1993), suggesting CO_2 effects vary among cultivars. In addition, tests with radish showed that CO_2 partial pressures as high as 1000 Pa had no effect on storage hypocotyl (radish) dry mass for cvs. Cherry Belle and Giant White Globe, but storage hypocotyl dry mass was reduced with cv. Early Scarlet Globe (Mackowiak et al., 1994). Collectively, these results suggest that CO_2 partial pressures in the 500 to 1000 Pa range can be supraoptimal for yield, with the degree of yield depression being dependent upon the species and cultivar. Super-elevated CO_2 partial pressures have not been studied for potato, a species that is a prime candidate for a CELSS. In this paper we report on the response of two cultivars of potato grown from plantlets to maturity in controlled environmental chambers maintained at four different CO_2 partial pressures that are applicable to a CELSS.

Materials and Methods

Environmental Conditions

Four 105 day studies were conducted with potato (*Solanum tuberosum* L.) cvs. Denali and Norland grown in a 1.8 m × 2.4 m environmental growth chamber (EGC Inc., Chagrin Falls, OH, USA). Each study was designed as a single CO_2 treatment to maintain one of the following partial pressures: 50, 100, 500, or 1000 Pa CO_2 ± 7 % (CV) of the set point. All studies were conducted at the Kennedy Space Center (KSC), FL, USA, where normal atmospheric pressure is approximately 101 kPa; thus treatments corresponded to concentrations of 500, 1000, 5000 and 10,000 µmol mol^{-1}, at standard conditions. The 50 Pa treatment was chosen over the normal ambient (36 Pa) to eliminate periodic CO_2 fluctuations resulting from human activity around the growth chamber. Carbon dioxide concentrations within the growth chamber were monitored with an infrared gas analyzer (Anarad Inc., Santa Barbara, CA, USA) and controlled by a dedicated computer system. Partial pressures were maintained by continuously adding CO_2 to the chamber to achieve at least 75 % of the treatment value, which was supplemented with computer controlled injections of additional CO_2 to maintain the appropriate partial pressure. Control-system calibrations were performed automatically each day using a zero-gas (nitrogen) and a span-gas near the working partial pressure for each study. As a check on the infrared analyzer values, atmospheric samples from the chamber were periodically analyzed for CO_2 using a gas chromatograph with a thermal conductivity detector.

Lighting in the chamber was provided by thirty 2.44 m, 1.5 A Vita-Lite fluorescent lamps (Duro-Test Inc., North Bergen, NJ, USA). Lamps were cycled to provide a 12 h light/12 h dark photoperiod. Photosynthetic photon flux (PPF) was measured at weekly intervals with a quantum sensor (Model 190, LI-COR Inc., Lincoln, NE, USA) at the canopy level and averaged 257 ± 12, 248 ± 31, 265 ± 32, and 244 ± 38 µmol m^{-2} s^{-1} for the 50, 100, 500, and 1000 Pa CO_2 treatments, respectively. This provided a daily PPF of 11.1, 10.7, 11.4, and 10.5 mol m^{-2} d^{-1}. Temperatures for all tests averaged 20.0 ± 0.4 °C during the light period and 15.7 ± 0.5 °C during the dark period. Relative humidities were constant during the light/dark cycle and averaged 61 ± 5 %.

Plant culture

Nodal-propagated sterile culture plantlets of cvs. Denali and Norland were transplanted into slits of white/black plastic sheets that covered 0.25 m^2 plastic culture trays (Wheeler et al., 1990). Trays and plantlets were covered with white acrylic germination covers to aid acclimation; these were removed three days after planting (DAP). Plants were thinned from three to either one or two plants per tray by 12 DAP, resulting in two trays per CO_2 and density treatment. At 14 DAP, each tray was enclosed with a 60-cm high, white vinyl-coated fencing (5 cm × 6.2 cm holes) to confine shoot growth to approximately 0.3 m^2 area. This provided planting densities of approximately 3.3 or 6.7 plants m^{-2} for trays with 1 or 2 plants per tray.

A modified half-strength Hoagland nutrient solution (Hoagland and Arnon, 1950) was used, where nutrient solution was continuously recirculated between a single reservoir and eight culture trays. Water was replenished by manually adding deionized water to the reservoir each day to maintain a constant volume (80 L), based on a sight gauge. Water uptake per CO_2 treatment was calculated as a summation of water used by all plants in the growth chamber since all trays shared a single reservoir. This assured that all plants experienced the same nutrient solution. WUE was determined by dividing the total biomass per CO_2 trial (pooling density and cultivar data) by the total amount of water and nutrient solution volumes added to the nutrient reservoir. Nutrients depleted from the solution were replenished twice each week, using a concentrated stock solution. Nutrient replenishment was based on measurements of total water use and a nutrient solution electrical conductivity of 0.12 S m^{-1}. Elemental concentrations of the solution were monitored weekly using atomic absorption and inductively-coupled plasma spectroscopic techniques to ensure adequate nutrition throughout the studies. Solution pH was continually monitored and controlled automatically to 5.8 with additions of 0.39 mol L^{-1} HNO_3.

Beginning at 35 DAP, stomatal conductance measurements of three upper-canopy leaves (abaxial surface only) from each tray (3 samples per tray or 12 samples per cultivar) were taken at weekly intervals with a steady-state porometer (Model LI-1600, LI-COR Inc., Lincoln, NE, USA) during the sixth hour of the light period. Stomatal conductance data were not separated by planting density treatment since density had no apparent effect on the unshaded, upper canopy leaves. For measurements taken at 50 Pa CO_2, a mask was worn connected by plastic tubing to a vacuum pump outside the chamber for venting exhaled breath and preventing any transient increases in CO_2. No venting was neccessary during measurements at 100, 500, and 1000 Pa treatments. At 105 DAP, plants were harvested and separated into shoots (leaves + stems), roots, and tubers >0.5 cm. All tissues were oven-dried for at least 48 h at 70 °C and then weighed. Harvest index (HI) was calculated as tuber dry mass/total plant dry mass.

Data Analysis

One tray of plants was considered a subsample in each CO_2 treatment and planting density, resulting in two subsamples per treatment. Due to the lack of CO_2 replicates, only treatment means are presented. Likewise, stomatal conductance data for CO_2 treatments are presented as averages ± standard errors. Since unshaded, upper canopy leaves were sampled for stomatal conductance, plant density was not a likely factor in this measurement and was not analyzed. Repeated measures ANOVA was used to compare leaf conductance patterns over time within CO_2 treatments.

Results and Discussion

Harvest

Combined harvest data for both planting densities and both cultivars are shown in Fig. 1. Shoot biomass increased linearly as the CO_2 partial pressure increased, where biomass was approximately 30 % greater at 100 versus 50 Pa treatment (Fig. 1). The linear increase with increased CO_2 suggests that

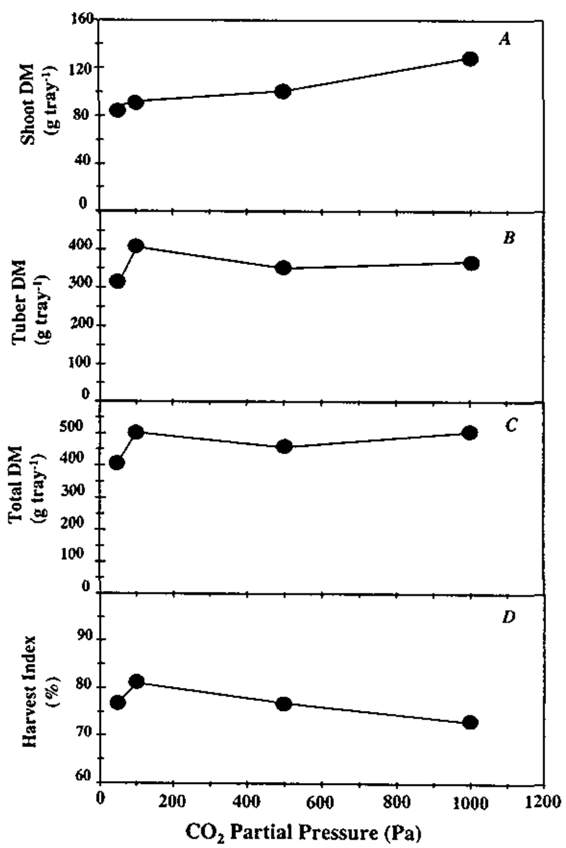

Fig. 1: Effect of carbon dioxide on A, shoot dry mass (DM); B, tuber DM; C, total DM; D, harvest index of potato. Data represent averages of two cultivars and two planting densities. Plants were grown in hydroponic culture trays, allowing approximately 0.4 m^2 $tray^{-1}$ of exposed canopy.

shoot biomass may continue to increase even beyond 1000 Pa CO_2. In addition, shoot biomass was greater at the higher density (131 vs. 73 g $tray^{-1}$) and cv. Denali produced 115 vs. 90 g $tray^{-1}$ for cv. Norland (data not shown).

In contrast to shoot biomass, tuber DM tended to decline after reaching a high value at 100 Pa CO_2 (Fig. 1). Previous studies with potato under 400 and 800 $\mu mol\, m^{-2} s^{-1}$ PPF resulted in greater tuber yields at 100 than 35 Pa CO_2 but levels greater than 100 Pa were not tested (Wheeler et al., 1991). Even though CO_2 partial pressures as great as 1000 Pa were not deleterious to tuber yields, chlorotic/necrotic areas were seen on leaves sooner than normally expected, suggesting some minor damage may have resulted from the very high CO_2. Recent studies with potato grown in elevated CO_2 and high PPF have shown that starch unloading does not keep pace with starch synthesis, resulting in possible leaf damage (Stutte et al., 1996). Concentrations as great as 1700 Pa (20,000 $\mu mol\, mol^{-1}$) CO_2, resulted in decreased seed yield in wheat, relative to yields at 85 Pa (1000 $\mu mol\, mol^{-1}$) CO_2 (Bugbee et al., 1994). In addition, concentrations above 100 Pa CO_2 resulted in reduced soybean yields when compared to 500 Pa (Wheeler et al., 1993). Thus, there are similarities between super-elevated CO_2 effects on tuber yield in our study and CO_2 effects on wheat and soybean seed yields. However, further studies are needed to determine if those similarities would persist at even greater partial pressures or at different combinations of PPF and CO_2. Tuber yield for all CO_2 treatments was greater at the higher density planting (451 g $tray^{-1}$) than at the lower density planting (267 g $tray^{-1}$), while cv. Denali produced an average of 399 g $tray^{-1}$ and cv. Norland produced 319 g $tray^{-1}$. Root + stolon DM made up a small portion of the total DM (< 2 %), and showed no apparent trends relative to CO_2 partial pressure.

Total biomass tended to plateau after reaching 100 Pa CO_2 (Fig. 1). As with the other parameters, the higher density planting produced more total biomass on average (591 vs. 345 g $tray^{-1}$) and cv. Denali had more total biomass (521 vs. 414 g $tray^{-1}$) than cv. Norland. These trends are consistent with other CO_2 response studies where potato was tested at lower partial pressures (Wheeler et al., 1989, 1991).

As result of increased shoot dry mass and a flattening of the tuber biomass curve at very high CO_2, the harvest index (HI) tended to decrease after reaching 100 Pa CO_2 (Fig. 1). Thus, unlike moderate CO_2 enrichment (100 Pa), partitioning to tubers appears to be negatively affected by very high CO_2 partial pressures (500 and 1000 Pa). Density and cultivar had no effect on HI values, where high density vs. low density values were 76 and 78 % HI, respectively. Both cultivars had an average HI of 77 %. The HI depression at super-elevated CO_2 was similar to what was seen with soybean (Wheeler et al., 1993).

Doubling the planting density from 1 to 2 plants per tray improved average yields 40 % and would be worth implementing in a CELSS. Under the environmental conditions of this study, cv. Denali produced more tuber biomass than Norland and would appear to be the cultivar of choice. However, Denali is a later maturing cultivar relative to Norland and may not perform as well if the growth cycle was reduced by a few weeks. Although plants were confined to a 0.3 m^2 area by wire cages around the trays, plants still received side lighting; hence, using cross-sectional areas alone would underestimate total PPF to the plants. Assuming conservatively that each tray had an available area of 0.4 m^2 (Wheeler et al., 1990), total crop growth rates and tuber growth rates can be estimated by dividing DM per tray by 0.4 m^2 and 105 days (Table 1). Dividing the growth rates again by daily PPF values indicates a PPF conversion efficiency up to 1.22 g mol^{-1} (100 Pa plants) for total biomass and 0.98 g mol^{-1} for tuber DM. These values are higher than conversion efficiencies reported for potato stands grown at 100 Pa CO_2 and at a higher PPF of 800 to 900 µmol $m^{-2} s^{-1}$ (Wheeler et al., 1996). The discrepancy between conversion efficiences at low versus high PPF may reflect errors in estimating total light reaching the plants, but is consistent with measurements of high quantum yield at low irradiance (Radmer and Kok, 1977).

Stomatal Conductance

Porometer measurements throughout growth showed that Norland stomatal conductance was greatest at 1000 Pa. Conductance was greatest for Denali at 500 Pa (Fig. 2). Conductance of both cultivars decreased as CO_2 partial pressure was increased from 50 to 100 Pa (Fig. 2). There have been several reports describing reversal of stomatal closure at very high partial pressures; for example, tomato (Hickleton and Jolliffe, 1980), cotton (Pallas, 1965), cucumber (Pfeufer and Krug, 1984), and soybean (Pallas, 1965; Wheeler et al., 1993), but the mechanism(s) responsible for these observations are not known. It is possible that there may be a direct influence of CO_2 on intracellular pH (Bown, 1985), leading to greater K^+ uptake by the guard cells, resulting in stomatal opening (Tallman, 1992). However, this hypothesis is inconsistent with stomata remaining closed during dark periods when respiration would be expected to increase internal CO_2 partial pressures. There may be interactions between high, external (ambient) CO_2 and diurnal light cycles that affect guard cell opening.

Repeated measures ANOVA of each cultivar found significant age effects, where a relatively steep increase in upper canopy stomatal conductance occurred during early growth, followed by a gradual decline for most treatments over the growing cycle (Fig. 3). This is a common pattern for many plant species (Field, 1987). Conductance values were greatest at about 6–7 weeks into the study. After this, conductance declined over time for the 50 and 100 Pa CO_2 treatments (Fig. 3), but remained relatively high for the 500 and 1000 Pa treatments, particularly for cv. Norland. All treatments showed relatively stable stomatal conductance between 10- to 14-weeks-age.

Table 1: Growth and photon conversion efficiencies of potato at 100 Pa CO_2.

Cultivar	PPF	Growth Rate		Conversion Efficiency	
		Tuber	Total Plant	Tuber	Total Plant
	mol $m^{-2} d^{-1}$	g $m^{-2} d^{-1}$	g $m^{-2} d^{-1}$	g mol^{-1} PPF	g mol^{-1} PPF
Norland	10.76	8.83	10.95	0.82	1.02
Denali	10.67	10.43	12.98	0.98	1.22

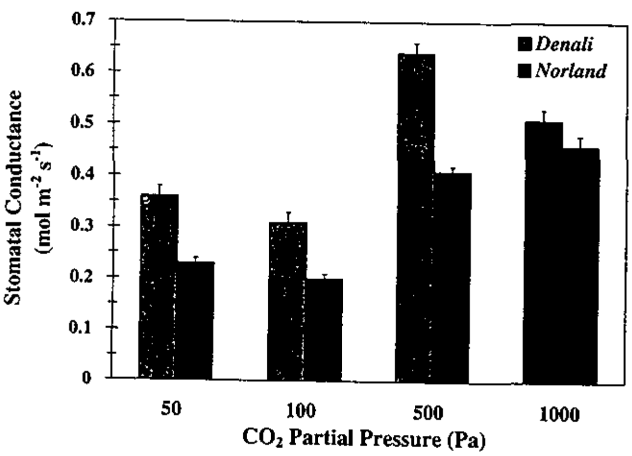

Fig. 2: Average effect of carbon dioxide on stomatal conductance of upper canopy leaves of potato cvs. Denali and Norland. Each bar represents the mean of weekly measurements taken from 5 to 14 weeks (n = 120). Vertical bars indicate standard errors.

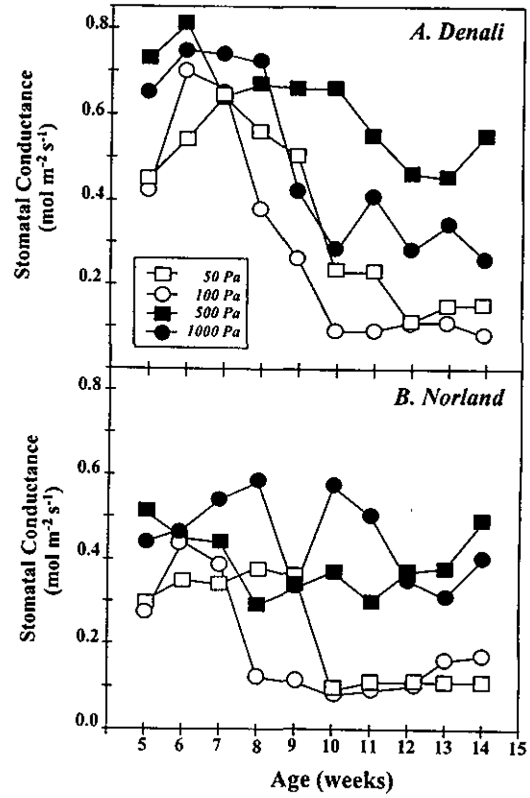

Fig. 3: Effect of carbon dioxide on stomatal conductance of upper canopy leaves of potato cvs. Denali (A) and Norland (B) over time. Each symbol represents the mean of weekly measurements (n = 12).

Water Use

Daily water uptake at all CO_2 partial pressures increased at similar rates until about day 42, which coincided approximately with full canopy coverage. Following this, water uptake

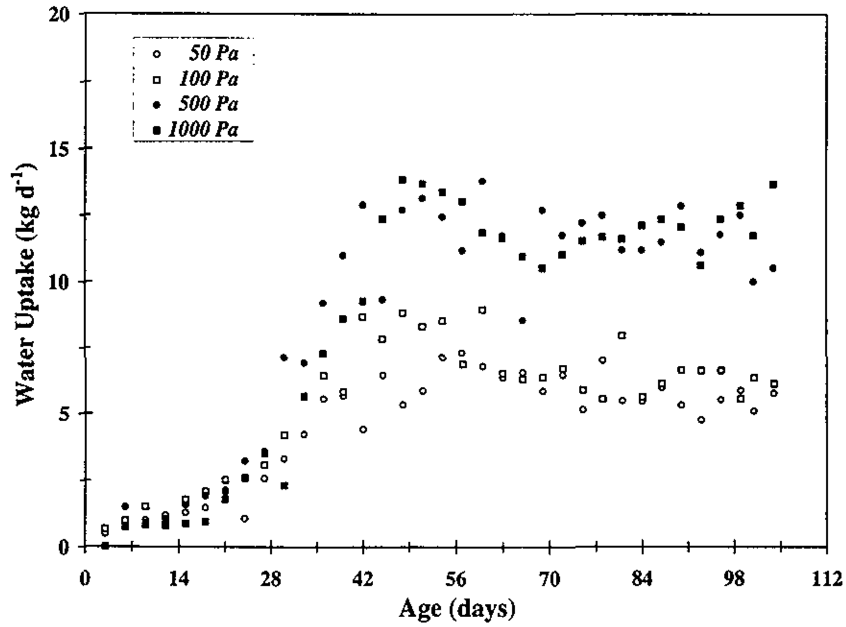

Fig. 4: Effect of carbon dioxide on water uptake by potato plants grown in nutrient film technique (NFT) systems. Data represent running averages of 3 d intervals. Total enclosed canopy area was approximately 3.2 m^2.

Table 2: Effect of CO_2 on stomatal conductance, water uptake, and total biomass production of potato plants during 15-week studies.

CO_2 Pa	Stomatal Conductance[a] mol m^{-2} s^{-1}	Water Uptake kg	Total Biomass kg	Water Use[b] Efficiency g kg^{-1}
50	0.29	542	3.25	6.0
100	0.25	573	4.02	7.0
500	0.52	963	3.66	3.8
1000	0.48	1062	4.04	3.8

[a] Stomatal conductance of the upper canopy leaves averaged for both cultivars from 5 through 14 weeks.
[b] Expressed as g biomass (DM) produced per kg water used.

remained relatively constant for the 50 and 100 Pa treatments, but continued to increase for another week for the 500 and 1000 Pa treatments (Fig. 4). The increased water use is further evidence for the effect of higher stomatal conductance at super-elevated CO_2. Assuming 0.4 m^2 per tray (8 trays per CO_2 treatment), water uptake rates by day 50 were about 2 kg m^{-2} d^{-1} for the lower CO_2 treatments (i.e., 50 and 100 Pa) and 4 kg m^{-2} d^{-1} for the higher partial pressures (i.e., 500 and 1000 Pa). Studies with soybeans grown under similar conditions (except for warmer temperatures) showed similar trends in water uptake in response to CO_2 (Wheeler et al., 1993).

Water use efficiency (WUE) improved when the CO_2 partial pressure was increased from 50 to 100 Pa (Table 2), which is consistent with observations from related studies (Eamus, 1991; Wheeler et al., 1993). However, plants grown at 1000 Pa CO_2 used almost twice as much water as the 100 Pa treatment, resulting in a 46% decrease in WUE compared to 100 Pa CO_2 and a 37% decrease compared to the 50 Pa treatment (Table 2).

Total plant dry mass was greatest for the 1000 Pa treatment, but correlation with water uptake was low (r = 0.36). Correlation between water uptake and leaf conductance was high (r = 0.95). If conductance data are transformed to account for total leaf area by using shoot dry mass data, (shoot DM × stomatal conductance), the correlation with water uptake is even greater (r = 0.99), which is similar to findings reported for soybean grown under similar conditions (Wheeler et al., 1993). It is interesting to note the conductance of 500 and 1000 Pa treatments did not decline much over time, as though stomata remained open (Fig. 3). Although it was not measured in this study, related studies have shown that dark-period conductance remained high when potato plants were grown at 500 and 1000 Pa CO_2 (Mackowiak et al., 1992), which may have contributed to increased water uptake at the highest CO_2 levels.

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References

Bennett, S. M., T. W. Tibbitts, and W. Cao: Diurnal temperature fluctuation effects on potatoes grown with 12 h photoperiods. Amer. Pot J. *68*, 81–86 (1991).

Bown, A. W.: CO_2 and intracellular pH. Plant Cell and Environ. *8*, 459–465 (1985).

Bugbee, B., B. Spanarkel, S. Johnson, O. Monje, and G. Koerne: CO_2 crop growth enhancement and toxicity in wheat and rice. Adv. Space Res. *11*, 257–267 (1994).

Cao, W. and T. W. Tibbitts: Physiological responses in potato plants under continuous irradiation. J. Amer. Soc. Hort. Sci. *11*, 525–527 (1991).

– – Growth, carbon dioxide exchange and mineral accumulation in potatoes grown at different magnesium concentrations. J. Plant Nutri. *15*, 1359–1371 (1992).

Eamus, D.: The interaction of rising CO_2 and temperatures with water use efficiency. Plant Cell and Environ. *14*, 843–852 (1991).

ENGELS, C. H. and H. MARSCHNER: Allocation of photosynthate to individual tubers of *Solanum tuberosum* L. I. Relationship between tuber growth rate and enzyme activities of the starch metabolism. J. Exp. Bot. *37*, 1795–1803 (1986a).

– – Allocation of photosynthate to individual tubers of *Solanum tuberosum* L. II. Relationship between growth rate, carbohydrate concentration and ^{14}C-partitioning within tubers. J. Exp. Bot. *37*, 1804–1812 (1986b).

– – Allocation of photosynthate to individual tubers of *Solanum tuberosum* L. III. Relationship between growth rate of individual tubers, tuber weight and stolon growth prior to tuber initiation. J. Exp. Bot. *37*, 1813–1822 (1986c).

EWING, E. E. and P. C. STRUIK: Tuber formation in potato: Induction, initiation, and growth. Horticultural Reviews. *14*, 89–198 (1992).

FIELD, C. B.: Leaf-age effects on stomatal conductance. In: ZEIGER, E., G. D. FARQUHAR, and I. R. COWAN (eds.): Stomatal function, pp. 366–384. Stanford University Press (1987).

HANNAPEL, D. J.: Characterization of the early events of potato tuber development. Physiol. Plant. *83*, 568–573 (1991).

HICKLETON, P. R. and P. A. JOLLIFFE: Alterations in the physiology of CO_2 exchange in tomato plants grown in CO_2-enriched atmospheres. Can. J. Bot. *58*, 2181–2189 (1980).

HOAGLAND, D. R. and D. I. ARNON: The water-culture method for growing plants without soil. Univ. Calif. Exp. Sta. Cir. 347 (1950).

MACKOWIAK, C. L., R. M. WHEELER, and N. C. YORIO: Increased leaf stomatal conductance at very high carbon dioxide concentrations. HortSci. *27*, 683 (1992).

MACKOWIAK, C. L., L. M. RUFFE, N. C. YORIO, and R. M. WHEELER: Effect of carbon dioxide enrichment on radish production using nutrient film technique (NFT). NASA Tech. Mem. 109198 (1994).

PALLAS, J. E.: Transpiration and stomatal opening with changes in carbon dioxide content of the air. Science *147*, 171–173 (1965).

PFEUFER, B. and H. KRUG: Effects of high CO_2-concentrations on vegetables. Acta Hort. *162*, 37–44 (1984).

RADMER, R. and B. KOK: Photosynthesis: Limited yields, unlimited dreams. BioScience. *27*, 599–604 (1977).

STEWARD, F. C., U. MORENO, and W. M. ROCA: Growth, form and composition of potato plants as affected by environment. Ann. Bot. *48*, 1–45 (1981).

STUTTE, G. W., N. C. YORIO, and R. M. WHEELER: Interacting effects of photoperiod and photosynthetic photon flux on net carbon assimilation and starch accumulation in potato leaves. J. Amer. Soc. Hort. Sci. (in press).

TALLMAN, G.: The chemiosmotic model of stomatal opening revisited. Crit. Rev. Plant Sci. *11*, 35–57 (1992).

TIBBITTS, T. W. and W. CAO: Use of potatoes in bioregenerative life support systems. Int. Conf. Life Support and Biospherics, Proceedings. pp. 285–294 (1992).

WALWORTH, J. L. and J. E. MUNIZ: A compendium of tissue nutrient concentrations for field-grown potatoes. Amer. Pot. J. *70*, 579–597 (1993).

WHEELER, R. M. and T. W. TIBBITTS: Utilization of potatoes for life support systems in space. I. Cultivar-photoperiod interactions. Amer. Potato J. *63*, 315–323 (1986a).

WHEELER, R. M., K. L. STEFFEN, T. W. TIBBITTS, and J. P. PALTA: Utilization of potatoes for life support systems in space. II. The Effects of temperature under 24-h and 12-h photoperiods. Amer. Potato J. *63*, 639–647 (1986b).

WHEELER, R. M. and T. W. TIBBITTS: Utilization of potatoes for life support systems in space. IV. Effect of CO_2 enrichment. Amer. Potato J. *66*, 25–34 (1989).

WHEELER, R. M., C. L. MACKOWIAK, J. C. SAGER, W. M. KNOTT, and C. R. HINKLE: Potato growth and yield using nutrient film technique (NFT). Amer. Potato J. *67*, 177–187 (1990).

WHEELER, R. M., T. W. TIBBITTS, and A. H. FITZPATRICK: Carbon dioxide effects on potato growth under different photoperiods and irradiance. Crop Sci. *31*, 1209–1213 (1991).

WHEELER, R. M., C. L. MACKOWIAK, L. M. SIEGRIEST, and J. C. SAGER: Supraoptimal carbon dioxide effects on growth of soybean [*Glycine max* (L.) Merr.]. J. Plant Physiol. *142*, 173–178 (1993).

WHEELER, R. M., C. L. MACKOWIAK, G. W. STUTTE, J. C. SAGER, N. C. YORIO, L. M. RUFFE, R. E. FORTSON, T. W. DRESCHEL, W. M. KNOTT, and K. A. COREY: NASA's biomass production chamber: A testbed for bioregenerative life support studies. Adv. Space Res. *18*, 215–224 (1996).